

# ANNALS OF NATURAL HISTORY.

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XXV.—*On the recent Doctrines of Vegetable Embryology.*

By HERBERT GIRAUD, Member of the Council of the Botanical Society of Edinburgh, Ext. Mem. Med. Soc. Edin.

[With a Plate.]

NOTWITHSTANDING the rapid progress which has of late been made in developing the phænomena attendant on the reproduction of plants, still the true theory of phanerogamic embryology has not yet been fully established. The discoveries of Amici, Brown, and Brongniart, proceeding so far in advance of the old doctrines of Kælreuter, Gärtner and Linnæus, gave, as it were, a fresh impulse to the inquiry regarding the intimate nature of the origin and development of the embryo in flowering plants; hence, in this country, but more particularly on the continent, this subject has been prosecuted with considerable zeal and activity; and it has certainly received much elucidation by the disclosure of phænomena hitherto little suspected. Still, however, the statements of some of the most eminent of the continental phytologists are of a very opposite nature, and the hypotheses to which they would justly lead, are still more widely discrepant. I here allude to the very discordant opinions, regarding the origin of the embryo, entertained by Schleiden, Wydler, and many of the German botanists on the one hand, and the views maintained by Mirbel, Spach, and Brongniart on the other.

The facts and doctrines advanced by Schleiden and his followers have been made known to British botanists chiefly through the medium of a translation by Dr. Wood of Bristol, published in the L. and Ed. Philosophical Magazine for March 1838; as, however, some of the readers of this paper may not yet be aware of the views of Schleiden, I will venture shortly to detail them; that a general view may be taken of the disputed points and of the question as it at present stands. According

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to this observer\*, at a very early period of the development of the ovule, a cellule from the interior of the nucleus, which originally differed not from the surrounding ones, is developed to an extraordinary degree, and presses more or less on the surrounding tissue of the nucleus, which is then absorbed from within outwards. This cellule is the embryo-sac (membrana amnii, Malpighi; sac-embryonnaire, Brongniart; quintine, Mirbel) which exists in all phanerogamic plants without exception, even before impregnation. This embryo-sac contains a substance which is gradually transformed into cellular tissue; and being ultimately developed within the embryo-sac, forms (when not absorbed by the growth of the embryo) the endosperm, or albumen of most authors. The pollen tube, having made its way through the conducting tissue of the stigma, and having reached the ovule, penetrates the aperture in the teguments, traverses the summit of the nucleus, and following the intercellular passages arrives at the embryo-sac. Having reached this point the pollen tube presses before it the membrane of the embryo-sac, which is then folded all around it; so that the extremity of the pollen tube appears to penetrate into the sac; though in reality it is on the outside of it. (Pl. IV. fig. 1. and 2.) Thus inclosed the extremity of the pollen tube enlarges into the form of an oval spheroid, and its contents are converted into cellular tissue; at its sides are formed the lateral organs or cotyledons, from which the extremity remains distinct and is developed into the plumule. The portion of the tube situated above the embryo, and which is embraced by a duplicature of the embryo-sac, is gradually but completely obliterated; so that the embryo is then left free within its sac. In this way the embryo is formed of two membranes;—the indented embryo-sac and the membrane of the pollen tube. (Fig. 2.) With these statements of Schleiden the still more recent observations of Wydler† agree, except as regards the folding in of the embryo-sac, which this last observer has never met with; but it appeared to him

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that the cavity of the sac elongated itself, under the form of a straight canal, even to the summit of the ovule, and there opened in the endostome and received the extremity of the pollen tube.

If the truth of these observations be admitted, two very obvious conclusions will result. 1st. Our notions regarding the functions of what are called the male and female organs (stamens and pistils) must be materially altered, and the sexes of the two sets of organs respectively exchanged; the anther must be considered as a female ovarium, and each pollen grain as the germ of a new organism, being determined in its development by the secretions of the embryo-sac; this last structure therefore must be held to correspond with the male organ. 2nd. The process described by Schleiden obviously establishes a close analogy in the development of the embryo between the phanerogamia and those cryptogamia in which the sporules appear to be conversions of the cellular tissue of the foliaceous organs; for the same part in both furnishes the groundwork of the new plant in each group.

It has been conceived by Dr. Carpenter\* that it is not the extremity of the pollen tube, but one of the pollen granules transmitted along the tube, which is ultimately developed into the embryo, and that hence a still more intimate analogy may be instituted between the reproductive organs of flowering and those of flowerless plants; a precisely similar function being performed by the theca and the anther, and by the spore and the pollen grain. These doctrines, so deeply affecting some of the most generally received opinions regarding the reproduction of flowering plants, have not passed without the critical investigations of other observers, but have incited MM. Mirbel and Spach to enter on a series of inquiries undertaken for the express purpose of testing the accuracy of the statements of Schleiden and Wydler. As far as I am aware, these observations have not yet been published, and are little known in this country; they were conducted with the view of ascertaining the intimate nature of the develop-

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ment of the embryo in *Zea Mays*. The following are the results which were obtained, arranged, as by Mirbel and Spach, under seven general heads, corresponding with the progressive periods of the growth of the female organs\*.

*First Period.*—The origin of the female spike of the *Zea Mays*, like that of all the external organs of plants, commences in a simple excrescence of cellular tissue, invisible to the naked eye. As it advances in age, this excrescence enlarges, elongates, becomes conical, and is studded partially from base to apex with little projections, which separately give origin to others. Each group of mammillary projections is the germ of a future flower; but seldom more than one becomes developed in each group, the rest being abortive. The remaining one, or that which is ultimately formed into a flower, produces at its circumference little thin cushions of tissue (bourrelets) in the form of rims, some of which form complete circles, others only semicircles; all however being concentric. Each of these little margins is quickly transformed into either a bract, a glume, a carpel, an ovary, or the integument of an ovule, according to the relative position which it occupies. The apex of the mammillary projection constitutes at this period the nucleus of the ovule.

*Second Period.*—The ovarium has now the form of a small cup with a large orifice, and its parietes consist of a thin and transparent membrane. The nucleus is fixed to the base of the ovarium;—an arrangement which is constant in the *Mays*. The primine and secundine proceed from the circumference of the nucleus, which they partly inclose. The first of these envelopes being much shorter than the other, surrounds the nucleus only at its base; hence it follows that the endostome sensibly extends beyond the exostome.

*Third Period.*—The style, of which, up to this period, there was not the least appearance, arises from that side of the ovarium which is nearest to the axis of the spike; as it elongates it assumes the form of a straight lamina of tissue. The ovule with its two membranes,—the primine and secundine, has

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now changed its position; its axis was at first parallel with that of the spike; but it is now inclined at an angle of about  $45^{\circ}$ . The secundine is still in advance of the primine.

*Fourth Period.*—The ovary is now of a rounded form, having its orifice narrowed into a kind of canal. The style continues to enlarge, and has its upper extremity terminated by two dentitions, more or less distinct, which may be considered as constituting a double stigma. The axis of the ovule now makes an angle of  $90^{\circ}$  or  $100^{\circ}$  with that of the ovarium, but coincides with that of the nucleus, at the apex of which it terminates. Very near this point, in the interior of the nucleus, there appears a small ovoid cavity, which contains a transparent mucous matter, first pointed out by Schleiden. (Fig. 4 *d.*) In the same ratio as the axis of the ovule inclines from that of the spike, do these portions of the primine and secundine, which lie on the opposite side, increase in size and elongate; while those portions which are attached to the side next the axis of the spike remain almost stationary in their development: from both these envelopes a process extends into the canal leading from the ovarium.

*Fifth Period.*—The ovarium continues to enlarge and the style to elongate; in the latter may be observed, as Brongniart first noticed, two bundles of tubes, which, after running together for a short distance, divide and pass off to each side of the ovarium, and continuing in a parallel direction, are ultimately lost in the dentiform projections which constitute the stigma. At this period the ovule is inclined at an angle of from  $125^{\circ}$  to  $135^{\circ}$ . The mucilage of the little cavity situated at the apex of the nucleus disappears; and at the same point may be distinctly seen a large ovoid, diaphanous utricle, which fills and lines the cavity. (Fig. 5 *a.*) This utricle is called by Mirbel the primary utricle. The fact of such an organ being formed, and of its having acquired a sensible progress in growth, before the period of impregnation, is of the greatest importance with reference to the views of Schleiden; this utricle is what is described by that observer as “l'extrémité antérieure du boyau pollenique.” It is surrounded by a thin projection, upon which are attached small spiral vesicles, arranged in close clusters; and it is terminated at its inferior

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extremity by a filiform tubular appendage, projecting at the endostome, and called by Mirbel the suspensor. This last organ is considered by Schleiden to be a portion of the pollen tube.

This early formation of the primary utricle, which may be considered as the first outline of the embryo, has been proved by Mirbel and Spach in a large number of the Gramineæ;—in all those, in fact, which they have examined.

*Sixth Period.*—Immediately after its first appearance the primary utricle contains a fluid opaque matter, in which however may be perceived an organized substance composed of globules having each a small central cavity; it is called by Mirbel “Globulo-cellular cambium.” This substance soon transforms itself into a mass of membranous tissue, which becomes moulded to the cavity of the primary utricle and its suspensor; this last organ now sensibly elongates and enlarges. (Fig. 6.)

*Seventh Period.*—It now becomes evident that the primary utricle, and the cellular tissue with which its cavity is filled, constitute the first trace of an embryo, which now enlarges at its thickest part, and elongates into a cellular lanceolate point; this is the lamina of the seminal leaf (hypoblaste, A. Richard; carnade, H. de Cassini), the inferior surface of which is in relation with the interior of the ovule, the superior with the axis of the spike; at its base is the radicle, terminated by an empty, flaccid, lacerated tube,—the last vestige of the suspensor, which has gradually been absorbed. Upon the upper surface of the lamina, immediately above the point at which it unites with the radicle, there is formed a projection or swelling of the tissue, which is the commencement of the plumule; it soon extends itself, and becomes imbedded in a kind of hood, in the cavity of which the first rudiments of the stem leaves make their appearance. The edges of this little hood gradually approach each other, unite, and form a kind of pouch\* (cotyledon, A. Richard and H. de Cassini). (Fig. 7. and 8.)

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In tracing out the development of the embryo in others of the Gramineæ, MM. Mirbel and Spach found the phænomena presented by each species to be so closely similar, that the embryogeny of the *Zea Mays* may justly be considered as the type of this process as carried on in all the Gramineæ: still however a few modifications of minor importance were disclosed; thus, in the *Zea Mays*, the *Euchlæna mexicana*, the *Coix Lacryma*, and in *Tripsacum hermaphroditum* the ovule remains attached to the base of the cavity of the ovarium, however advanced the period of development may be; but in *Sorgham vulgare* and *Melica nutans* the attachment of the ovule is so displaced that this body is found fixed to that internal portion of the wall of the cavity of the ovary which corresponds to its anterior surface. Again, in *Zea Mays*, and in *Euchlæna mexicana*, the apex of the ovule is inclined, and, as it begins to approach its base, the primine completely covers the secundine. About the same period those parts of the two envelopes which correspond with the orifice of the ovary, elongate into two empty points, of which one is inclosed within the other. Lastly, the primary utricule in *Euchlæna* differs from that of *Zea* and *Sorgham*, resembling a little crooked cone, the base of which is rounded; and the suspensor, which in *Sorgham* and *Zea* arises from the base of the utricule, and elongates itself in the direction of the axis to arrive at the exostome, arises in this instance from the side of the utricule, a little above its base; and in elongating towards the exostome it follows an oblique direction.

On comparing the observations of Schleiden and Wydler with those of Mirbel and Spach, which we have just stated in detail, a striking and essential difference is clearly perceptible between the conclusions to which these observations respectively lead, at the same time that a wide distinction is indicated between the doctrines necessarily flowing from each. In instituting a comparison between the conditions of the ovule and embryo during the progress of their development as stated by these observers, it will be found, that the parti-

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cular points upon which they do not agree, and with regard to which the statements of Mirbel and Spach would appear to controvert the views of Schleiden, may be ranged under three general heads, corresponding with as many stages of the development of the female organs.

1st. Schleiden maintains that when the axis of the ovule makes an angle of about  $90^\circ$  with that of the style, an oval cavity, containing a limpid mucous fluid, (cambium, Mirbel), is discovered near the apex of the nucleus; that the formation of this cavity is contemporaneous with that of the embryo-sac (quintine, Mirbel; sac-embryonnaire, Brongniart), which soon makes its appearance, gradually increases, and becoming filled with a cellular substance, occupies a considerable space in the nucleus. Now in opposition to this, M. Mirbel's investigations have shown, that the little cavity, which is always fixed to the apex of the nucleus, does not become enlarged during the growth of the ovule; but that its fluid contents soon contribute to the formation of the primary utricle.

2nd. It is asserted by Schleiden, that when the oval cavity enlarges and the embryo-sac is correspondingly developed, the tube issuing from the pollen grain penetrates to the summit of the nucleus, pressing before it the membrane of the embryo-sac, which, yielding to its pressure, forms a cæcum in which the extremity of the tube is lodged. This view is opposed by the statements of Mirbel, who has shown that in many species of plants, and particularly in the Gramineæ, the embryo-sac is wanting; and that in these cases the primary utricle takes its origin from the fluid matter (cambium) of the little cavity of the nucleus; so that this last may be wholly destitute of a lining membrane, such as Schleiden would make the embryo-sac. But even supposing that this part existed and underwent the changes conceived by Schleiden, and that a portion of the embryo-sac was expanded into a cæcum serving as a sheath for the extremity of the pollen tube, it would follow that from the translucency of the parts, the existence of two membranous expansions (the pollen tube and the embryo-sac) might readily be determined; but both Mirbel and Wydler have only succeeded in detecting one; that, namely, which

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3rd. Schleiden states that the part of the pollen tube lodged in the cæcum of the embryo-sac becomes club-shaped, and in its cavity is produced a mass of utricular tissue, with which it becomes filled; whilst the posterior part of the tube still continues in its original membranous condition; that portion soon disappears, while the extremity of the tube becomes transformed into the embryo, and commences a new development. Now M. Mirbel has shown that the first appearance of the primary utricle precedes the application of the pollen; that it is independently engendered in the ovule; and that, conjointly with the utricles which it produces, it commences the formation of the embryo. The same observer has moreover stated that the flaccid membranous tube by which the young radicle terminates, is not the posterior part of the pollen tube, but the suspensor, or appendage of the primary utricle, of which it evidently forms a part, as its elongation takes place from within outwards, and not from without inwards.

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of the nature of phanerogamic generation; for certainly the investigations of these latter observers lay more claim to our confidence than those of Schleiden, from their having been conducted with greater care, and in a regular chronological order\*. But with reference to this question, I believe that an induction may be drawn from a source, which, whilst it is derived from the most universal law of the development of plants, is free from those errors which will ever be found to creep into microscopical investigations, even when conducted by the most skillful hands.

From the recent additions which have been made to our knowledge regarding the morphology of the reproductive organs, I think it may be shown, that a consideration of the morphological conditions of the ovule and embryo, independent of arguments founded on any other grounds, would lead to the conclusion—that the embryo is originally a body foreign to the ovule, and introduced into it from without—a view corroborative of the opinions of Schleiden.

Most authors make four great stages in the morphology of the sexual system;—viz. the whorl of the calyx, corolla, stamens, and pistil. I think, however, we may make five or even six, by including what I believe to be leaf formations of the ovule. According to these authors, the upper and last stage of metamorphosis is that of the fruit-leaf (carpellary leaf), which, in each of its three dimensions, is changed in a peculiar way. But does the axis terminate with this carpellary whorl of leaf metamorphosis? Von Martius† is of opinion that the axile formation is terminated by the receptacle, upon which the fruit-leaf is situated; so that the elongation of the axis is herewith at an end. M. Mohl, found-

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ing, as I suppose, his opinion on the production of buds on the leaves of *Bryophyllum* and *Malaxis paludosa*, concludes that the ovules always spring from the upper surface and margins of a carpel leaf, and that they are wholly unconnected with the axis, which, as he supposes, has no share in the formation of the ovarium. Certainly the position of the ovules on the edges of the carpellary leaves in *Papaver* and others, or at the sides of the midribs in *Viola*, &c. would appear to favour these opinions.

Professor Meyen\* believes that the origin of the ovules is fourfold; that they originate most frequently at the margins of the carpellary leaves; next, at the sides of the midribs of the carpel leaves; and lastly, from the axis, where they occur either at the end of the axile formation, or at the side of the frequently much shortened axis. The facts, however, from which these statements are deduced, may be explained upon the supposition that the ovule is an axile formation; and if the ovula be considered as analogous to buds, they will fall in with that very general law—that a bud is never formed on a leaf, but from the axis or its derivative organs alone. The case of *Bryophyllum* alone offers a real exception to this view.

MM. Henry and Marquart† have represented the carpellary leaves separated from the axis and forming stamens, while nevertheless the axile formation produced ovules; than which no better proof can be afforded of the elongation of the axis. The most obvious conclusion regarding the nature of the true Placenta centralis libera is that it is a prolongation of the axis, as in the *Polygoneæ* and in *Taxus*; and Schleiden, who coincides in this view, enumerates several examples which tend to prove its correctness; such as the condition of the ovaria of the *Fumariaceæ* and *Cruciferæ*, and of the cones of the *Coniferæ*. Von Martius states that the reproductive organs produce axes of peculiar

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mination in the embryo; in which case, according to the general laws of vegetation, the embryo should be continuous, at its organic base, with the organic base of the ovule; and consequently the radicle should be turned towards the chalaza, that is to say, next the point where the ovular leaves (membranes) are connected; for in this way only can an organic continuity be established between the female parent plant and the embryo. But if the normal position of the embryo, with regard to the axis of the ovule, be considered, it will appear that in all these respects an opposite arrangement is presented; so that the organic base of the embryo (the radicle) is diametrically opposite to the organic base of the ovule (the chalaza), and is directed towards the micropyle. From this it is evident that the embryo cannot be considered as the product of metamorphosis within the ovule; that it has not taken its origin in the interior of that organ, but has been introduced into it from without, that it may attain a degree of development fitting it hereafter to live as an independent axis.

If this view be admitted, the doctrines of Schleiden will receive a confirmation, which must entitle them to more consideration than they would otherwise have merited, with the statements of Mirbel and Spach weighing so heavily against them; for the position which we have here maintained, on morphological grounds, is not liable to have its foundations shaken by those objections which may be raised against the observations both of Schleiden and of his opponents, from the well-known inaccuracies and deceptions which are attendant on microscopical investigations, however carefully conducted.

While then the accurate statements of Mirbel and Spach would appear to prove undoubtedly that the impregnation of the ovule is not required for the primary engendering of the first traces of the embryo, (which, if proved, would completely falsify the views of Schleiden and of Dr. Carpenter,) the morphological condition of that structure compels us to admit the high degree of probability which may be attached to the idea—that the embryo is a body origin-

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EXPLANATION OF PLATE IV.

*Fig. 1.* Part of the ovule and conducting tissue of *Phytolacca decandra*. *a.* Conducting tissue. *b.* Pollen tube. *c.* Embryo. *d.* Embryo-sac. *e.* Nucleus. *f.* Secundine. *g.* Primine. (Schleiden.)

*Fig. 2.* The extremity of the pollen tube (embryo) indenting the embryo-sac. *a.* Pollen tube. *b.* Embryo. *c.* Embryo-sac. (Schleiden.)

*Fig. 3.* The inferior part of an ovule of *Carduus nutans*, after impregnation. *a.* Pollen tube. *b.* Embryo. *c.* Embryo-sac. *d.* Nucleus. *e.* Teguments. (Schleiden.)

*Fig. 4.* Section of the ovarium of *Zea Mays* at an early period of its development. *a.* Primine. *b.* Secundine. *c.* Nucleus. *d.* The little cavity in which the primary utricle is afterwards formed. (Mirbel and Spach.)

*Fig. 5.* The same at a more advanced period. *a.* The primary utricle. (Mirbel and Spach.)

*Fig. 6.* The primary utricle, detached from the ovule, filled with the globulo-cellular cambium. (Mirbel and Spach.)

*Fig. 7.* The embryo detached. *a.* Cotyledon. *b.* The first leaf of the plumule. *c.* The second leaf of the plumule. (Mirbel and Spach.)

*Fig. 8.* The embryo at a more advanced period. *a.* The first leaf of the plumule. *b.* Radicle. *c.* The suspensor. (Mirbel and Spach.)

XXVI.—*Observations on the Family Helicidæ, and description of a new Genus.* By Dr. L. PFEIFFER of Cassel\*.

THE most difficult question concerning the limits of genera among the land mollusca has of late been frequently treated of, and with widely different results. If, on the one hand, Férussac went much too far, in comprising nearly all air-breathing mollusca with four tentacula in his genus *Helix*, still, on the other hand, the attempts at a division of this large group have not yet succeeded in a satisfactory manner. Draparnaud's genera, however, form a good basis, to which I am inclined with slight deviation to return. Lamarck evidently relied too much on individual peculiarities of the shell, because he was not acquainted with a sufficient number of species in which the transitions of the forms may be distinctly

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